

Delayed seed dispersal species and related traits in the desert of the United Arab Emirates

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Abstract: The ability of plants to safely retain seeds in the mother plant is an adaptive mechanism described in many desert plants. However, research about delayed seed dispersal species in the desert of the United Arab Emirates (UAE) is lacking. This study aims to identify these delayed seed dispersal species and assess the relationships of the presence of delayed seed dispersal with plant growth form, habit, spatial dispersal, antitelechoric mechanism, and seed release time. The relationships between the presence of delayed seed dispersal and the above studied traits were assessed by using the Pearson Chi-square test and Nonlinear Principal Components Analysis (NLPCA). Results showed that a total of 46 delayed seed dispersal species were recorded (15.0% of 307 studied species) and the highest incidence occurred in the Fabaceae family (17.4%). Delayed seed dispersal species were predominantly perennial plants (73.9%) with spatial restricted dispersal (67.4%), which released seed in the dry season (45.7%). The dominant groups of delayed seed dispersal species were persistent fruits species and synaptospermy (28.3%). All graminoids showed persistent lignified fruits, while prostrate annuals were basicarpic species with myxospermy. Sandy habitats had the highest number of delayed seed dispersal species (54.3%), whereas salt flats had the lowest (23.9%). In the desert of the UAE, delayed seed dispersal species spread seeds until the end of the dry and windy season, thus breaking seed dormancy at this time and ensuring seed germination in the next arrival of the rainy season. This morphological and ecological adaptation of delayed dispersal species is essential to the survival and sustainable development of vegetation in desert environments.

Keywords: Arabian desert; delayed dispersal; restricted dispersal; persistent fruits; seed release time; myxospermy; synaptospermy

1 Introduction

Many desert plants retain the seeds within the maternal tissue in dry fruits such as capsules or schizocarps, lignified fruits, or dry flowering scape that could detach in parts from the mother plant or shed seeds continuously for many months or even years when enough moisture softens the seed-retaining structure (Martínez-Berdeja et al., 2015). The ability of plants to retain seeds in

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Received 2021-06-01; revised 2021-09-06; accepted 2021-09-14

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the mother plant, which allows plants to reduce risk by retaining seed safely within protected maternal structures, is a frequent adaptive mechanism described in Mediterranean (Gutterman, 1994, 2002; Navarro et al., 2009a, b), Asian (Liu et al., 2014; Zhao et al., 2017), and American (Barrera et al., 2020) deserts. Generally, the retention of seeds on the mother plant is associated with seed releases (dispersal) triggered by environmental factors such as fire, drought or wetting (Lamont, 1991). The duration of mature seeds retained on the mother plant varies with the species and ecosystems according to Cowling and Lamont (1987), and Bastida and Talavera (2002) in the Mediterranean area, Ma and Liu (2008) in Asia, and Peters et al. (2009) in America.

Delayed seed dispersal species are distributed in different regions of the world, such as the Mediterranean (Navarro et al., 2009a, b), the Middle East (Gutterman, 2002), Australia (Groom and Lamont, 1998), North America (Martínez-Berdeja et al., 2015), Africa (Günster, 1992), and China (Gao et al., 2014). Gutterman and Ginott (1994) described 40 delayed seed dispersal species in the Negev (Israel) and Sinai (Egypt) deserts. Navarro et al. (2009a, b) identified 27 species with delayed dispersal in the arid mountains of the Moroccan Atlas, and 40 in the arid lands of southeastern Spain. In addition, Martínez-Berdeja et al. (2015) described 22 delayed seed dispersal species in the Mojave and Sonoran deserts in California, in which 11 are also found in the Central Namib Desert (Günster, 1992).

Delaying seed dispersal has many advantages (Lamont et al., 1991; Lamont and Enright, 2000), such as providing seed protection from predators (granivores) and/or abiotic stresses like drought, fire or lack of nutrients (Enright et al., 1998a, b; Martínez-Berdeja et al., 2015; Zhao et al., 2017). It is also considered as an adaptive mechanism to avoid the negative effects of competition from other species or sib competition (Borchert et al., 2003; Tapias et al., 2004). In the desert regions characterized by unpredictable climate, delaying seed dispersal until the arrival of favorable conditions (e.g., rainfall) for seed germination and seedling establishment is one of most important survival mechanisms (Gutterman and Ginott, 1994; Gao et al., 2014). In addition, seeds stored on mother plant are exposed to diurnal and seasonal fluctuations of rainfall, atmospheric moisture, wind, hydration-dehydration cycles, temperature, and light (Gao et al., 2014; El-Keblawy and Bhatt, 2015). These conditions could help break the dormancy of seeds and reduce germination requirements, thus resulting in a faster germination after dispersal (Gao et al., 2014; El-Keblawy et al., 2018).

Delayed seed dispersal is associated with plant life traits (e.g., plant habit and growth form) (Günster, 1994; Navarro et al., 2009a, b) and the mechanisms that prevent the dispersion of diaspore away from the mother plant, such as myxospermy, basicarpy and trypanocarpy, as shown in the Middle East desert (Gutterman, 1993, 1994, 2001), Arabian desert (Shabana et al., 2018), and Mediterranean region (Navarro et al., 2009a). Ellner and Shmida (1981) and Kamenetsky and Gutterman (1994) reported the relationships between herb growth form and delayed seed dispersal mechanism in the Negev Desert (Israel). Günster (1994) evidenced the predominance of delayed seed dispersal in annual species, compared with perennials in the Central Namib Desert. However, the desert of the Arabian Peninsula is characterized by extreme seasonality in rainfall and temperature; thus, the presence of delayed seed dispersal species and their relationships with other plant traits are less studied. The aims of this study are: (1) to identify the delayed dispersal species in the desert of the United Arab Emirates (UAE) and classify these species into groups based on the morphological structures that retain seeds on the plants, dispersal characteristics and diaspore traits; and (2) to explore the relationships between delayed seed dispersal species and plant traits (plant habit and growth form), spatial dispersal, antitelechoric mechanisms and seed release time. The results of this study could be important in understanding the importance of delayed dispersal as a plant survival mechanism in Arabian deserts.

2 Materials and methods

2.1 Study area

The UAE is located in the southeastern part of the Arabian Peninsula (22°40'N–26°00'N, 51°00'E–56°00'E). The desert of the UAE has a hyper-arid hot climate with two main seasons: a

rainy season with a mean temperature around 20°C from November to March, and a hot and dry season with a mean temperature ranging around 38°C from April to October. Humidity levels reach more than 90% in the hot and dry season. The average annual rainfall is around 110 mm with extreme variability in space and time (Böer, 1997; UAE Ministry of Environment and Water, 2015).

We focused on four types of habitats in this study: salt flats, gravel plains, sand sheets, and the Hajar Mountains (Jongbloed, 2003; Shabana et al., 2018). These habitats cover the main geomorphologic conditions in the UAE (Böer and Gliddon, 1997; Jongbloed, 2003). Salt flats (sabkha) separate the inland sandy areas and the low Arabian Gulf coast. Gravel plains are characterized by coarse sand and rocky soils dominated by *Acacia tortilis* and mixed with *Prosopis cineraria* and cultivated palms (*Phoenix dactylifera*). Sand sheets are dominated by the graminoids *Cyperus conglomeratus* and *Stipagrostis plumosa*, and the Hajar Mountains extend from the UAE to Oman with an elevation of 1000 m a.s.l.

2.2 Data collection

2.2.1 Species selection

Field sampling and observation were carried out monthly from May 2014 to October 2016. The data of delayed seed dispersal were obtained from 307 plant species (Shabana et al., 2018). These species account for 80% of the total flora in the desert of the UAE (Jongbloed, 2003; Karim and Fawzi, 2007a, b). There are 30 quadrates for each habitat and a total of 120 quadrates in this study (Shabana et al., 2018). Once the quadrates with the presence of delayed seed dispersal species were identified, a monthly monitoring was carried out for counting the duration of the fruits retained on the mother plant (Thanos, 2004). Voucher specimens of the studied species were retained in the Sharjah Seed Bank and Herbarium (Sharjah Research Academy, UAE).

2.2.2 Trait measurements

We classified these species into five groups described by Martinez-Berdeja et al. (2015) based on the morphological structure of retaining seeds on the mother plant, dispersal characteristic, and diaspore trait. The first group includes the species that produce flowers immediately above ground level and release their seeds in response to rainfall or sandstorm events, which corresponds to the "basicarpic species" described by Ellner and Shmida (1981). The second group, "gradually open capsules species", comprises species with woody branches that hold lignified capsules or calyx that open and gradually release seeds for more than one season. For these species, exposure to rainfall accelerates fruit opening (Walck and Hidayati, 2007). The third group, "species with schizocarpic fruits", are dry fruits developed from multiple carpels split into mericarps when mature. Sometimes, the mericarp is the dispersal unit and the diaspores are retained for a relatively long time (Shreve and Wiggins, 1964). The fourth group, "species with persistent fruits", is characterized by the presence of the persistent dried or fleshy indehiscent fruits retained for a long time. Finally, the fifth group, "species with persistent lignified fruits", includes the species that retain seeds in dry or persistent lignified fruits for long periods in the dried plant.

We measured spatial seed dispersal for each species according to the categories established by Ellner and Shmida (1981), Cain et al., (2000), and Navarro et al. (2009a). Species were considered as having developed spatial dispersal when equipped with structures that facilitate spatial dispersal such as pappi, barbs, or wings for dispersal by abiotic vectors e.g., wind; or fleshy fruits to disperse by biotic vectors e.g., vertebrate. Species were considered as having restricted dispersal if diaspores lacked such dispersal-enhancing characters (Willson, 1993).

For each species, we identified the antitelechoric mechanisms following van Rheede et al. (1999), which included synaptospermy, i.e., two or more seeds or one-seeded fruits joining together to form a compound diaspore (Ellner and Shmida, 1981; van Rooyen et al., 1990); myxospermy, i.e., the ability of a seed to produce mucilage upon hydration (van Rooyen et al., 1990; García-Fayos et al., 2010, 2013); and trypanocarp, i.e., dispersed fruit turning around,

creeping or drilling by hygroscopic movement (van Rooyen et al., 1990).

In order to describe the seed release time and seed storage time, we observed each species 10–12 times, with approximately 30–45-d intervals over a period of two years and six months.

Growth form and plant habit were also studied. To examine the plant habit, we classified the studied species according to Pérez-Harguindeguy et al. (2013), i.e., species with erect stems, species with prostrate stems (branches spreading or lying on the ground), and short basal species (leaves concentrated very close to the soil surface). Species were classified as perennial, annual and graminoids for the growth form. Species, family, habitats, delayed seed dispersal, plant traits (plant habit and growth form), seed storage time, seed release time, spatial seed dispersal, and antitelechoric mechanisms of the studied species are presented in Table S1.

2.3 Data analysis

A nonlinear principal component analysis (NLPCA) (De Leeuw, 1982) was used for comparison and representation of the results to identify the association between delayed seed dispersal (groups), plant traits (growth form and plant habit), spatial seed dispersal, antitelechoric mechanisms, seed release time and seed storage time. Bivariate relationships of studied traits were first assessed by Pearson correlation coefficient (r). Relationships between all studied traits and studied sites were assessed by Chi-square tests. For these last two treatments, the group "species with schizocarpic fruits" was not considered due to its low number of species. All statistical analyses were performed using SPSS 25.0 (SPSS Inc., USA).

3 Results

3.1 Number and groups of delayed seed dispersal species

A total of 46 delayed seed dispersal species were identified in our study, which represent around 15.0% of 307 studied species. These species belong to 22 families and 37 genera (Table S1). Fabaceae was the predominant species (8 species, 17.4% of total species). Perennial (shrubs) and annual herbs (41.3% and 23.9%, respectively) were the main growth form with greatest delayed seed dispersal species.

NLPCA analysis results distinguished the four major groups of delayed seed dispersal species: basicarpic, persistent fruits, gradually open capsules, and persistent lignified fruits (Fig. 1). The most dominant group of delayed seed dispersal was that contained persistent fruits species (13 species, 28.3%); followed by basicarpic, gradually open capsules, and persistent lignified fruits species (each represented by 9 species, 19.6%); and finally, schizocarpic fruits species (3 species, 6.5%). The first principal component accounted for 39.1% of variance and had high loadings from synaptospermy and spatial dispersal (Table 1). It separated species with developed spatial dispersal and synaptospermy (persistent fruits species) (e.g., *Zilla spinosa*, *Aerva javanica* and *Indigofera oblongifolia*) from species with restricted spatial dispersal (basicarpic species) (e.g., *Mesembryanthemum nodiflorum*; Table S1).

The second principal component accounted for 26.2% of the variance and had a high positive loading with main growth form, plant habit, and myxospermy (Table 1). It separated persistent lignified fruits species, which are mainly graminoids with erect habit and non-myxospermic (e.g., *Juncus* sp.) from the basicarpic species, which includes prostrate annual and myxospermic species (e.g., *Aizoon canariense*; Table S1). The Pearson correlations among traits are shown in Table 2: myxospermy and synaptospermy showed a significant correlation with spatial dispersal ($P < 0.001$). Myxospermy and seed release time also showed correlation with plant habit ($P < 0.050$).

3.2 Relationships between groups of delayed seed dispersal species and spatial dispersal

Delayed seed dispersal species mainly showed restricted spatial dispersal (31 species, 67.4%; Fig. 2). Basicarpic species (8 species), gradually open capsules species (9 species), and species with lignified persistent fruits (9 species) were restricted dispersal species. However, within persistent fruits species (13 species), only 5 species were restricted spatial dispersal and 8 species were developed spatial dispersal, i.e., dispersal with abiotic or biotic vectors (Fig. 2). Moreover, groups

of delayed seed dispersal species were significantly related to spatial dispersal patterns ($\chi^2=16.44$, $df=6$, $P<0.050$).

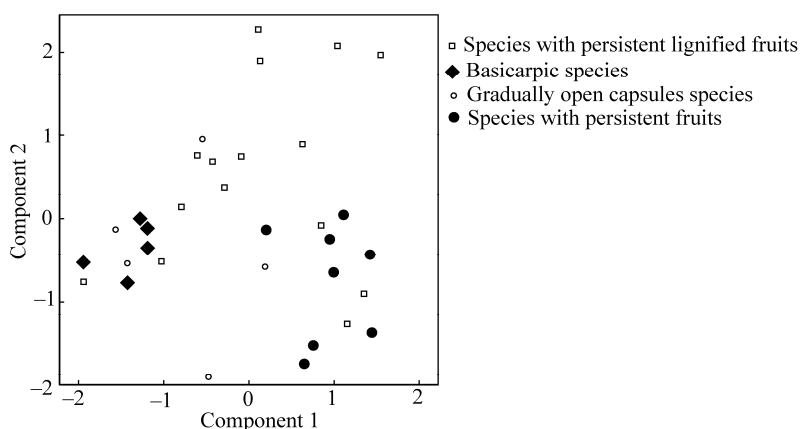


Fig. 1 Ordination plot of the 46 delayed seed dispersal species using Nonlinear Principal Components Analysis (NLPCA)

Table 1 Seven studied traits on the first two components of NLPCA

Trait	Component	
	1	2
Growth form	-0.177	0.616
Plant habit	0.277	-0.509
Seed release time	-0.178	0.078
Spatial dispersal	-0.541	-0.035
Myxospermy	-0.347	0.387
Synaptospermy	-0.742	-0.010
Trypanocarpy	-0.187	-0.007
Active total	3.125	2.095
Percentage of variance (%)	39.058	26.183

Table 2 Pearson correlations among studied traits

Trait	Plant habit	Seed release time	Growth form	Spatial dispersal	Trait	Plant habit	Seed release time
Plant habit	1.000						
Seed release time	-0.393*	1.000					
Growth form	-0.233*	-0.093	1.000				
Spatial dispersal	-0.206	0.097	-0.192	1.000			
Myxospermy	-0.620***	0.275	0.223	0.349*	1.000		
Synaptospermy	-0.292	0.143	-0.199	0.668***	0.404**	1.000	
Trypanocarpy	-0.082	0.161	-0.112	0.176	0.139	0.345*	1.000
Eigenvalue	1.829	1.013	0.888	0.500	0.356	0.342	0.134

Note: ***, $P<0.001$ level; **, $P<0.010$ level; *, $P<0.050$ level.

3.3 Relationships between groups of delayed seed dispersal species, growth form, and plant habit

Delayed seed dispersal species were predominantly perennial (28 species, 60.9%), followed by annuals (11 species, 23.9%) and graminoids (7 species, 15.2%). Groups of delayed seed dispersal species were significantly related with growth form ($\chi^2=41.36$, $df=6$, $P<0.001$). All graminoids species were persistent lignified fruits. Among perennials (28 species), 13 were persistent fruits species and 8 gradually open capsules species. Most of the annual species were basicarpy (63.0%; Fig. 3).

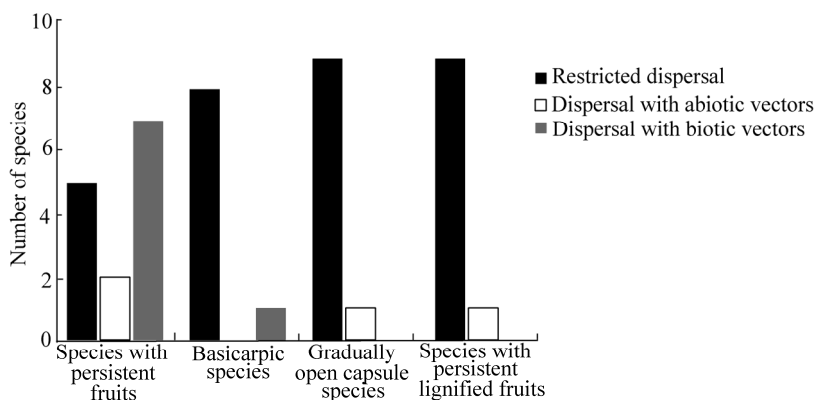


Fig. 2 Number of species in different spatial dispersal patterns and groups of delayed seed dispersal species

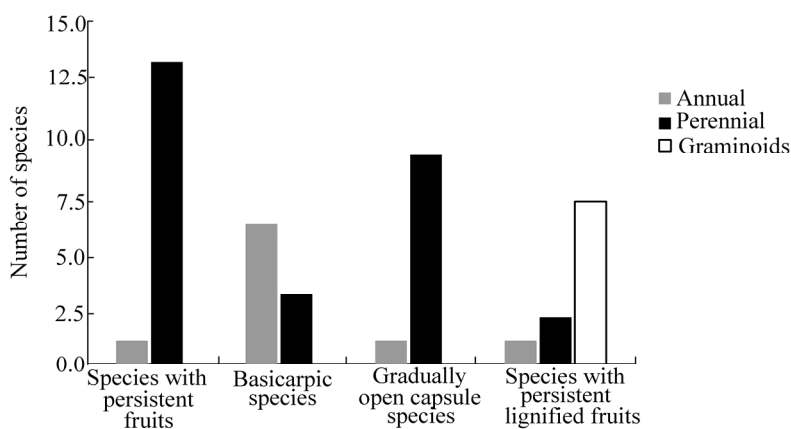


Fig. 3 Number of species in different growth form and groups of delayed seed dispersal species

Delayed seed dispersal species had erect habit (30 species, 65.2%), and 21.7% were prostrate (10 species) and 13.0% short basal plants (6 species). Groups of delayed seed dispersal species were significantly related with plant habit ($\chi^2=18.87$, $df=9$, $P<0.050$). Most basicarpic species were prostrate (80.0%). Erect habit was over-represented in persistent fruits species (11 species), followed by persistent lignified fruits species (9 species) and gradually open capsules species (7 species; Fig. 4).

3.4 Relationships between groups of delayed seed dispersal species and antitelechoric mechanisms

Among the three analysed antitelechoric mechanisms (myxospermy, synaptospermy, and trypanocarpy), synaptospermic (37.0%) and myxospermy (21.7%) were the most dominant within delayed seed dispersal species (Table 3). Relationships of delayed seed dispersal species with myxospermy and synaptospermy were significant ($P<0.050$; Table 3).

3.5 Relationships between groups of delayed seed dispersal species, seed storage, and seed release time

There was no significant relationship between delayed seed release groups and seed release time ($\chi^2=2.479$; $P>0.050$). Species that release their seeds in the dry season were more frequent (21 species), compared with those that released their seeds in rainy (9 species) and in both rainy and dry seasons (16 species; Table S1). There was no significant difference in the average number of months required for seeds to be released in different groups of delayed seed dispersal species. And the duration ranged between 8 months for basicarpic, persistent fruits, and persistent lignified fruits species, and 7 months for gradually open capsules species. The suitable release time of seeds occurred in the dry season for persistent fruits and schizocarpic fruits species.

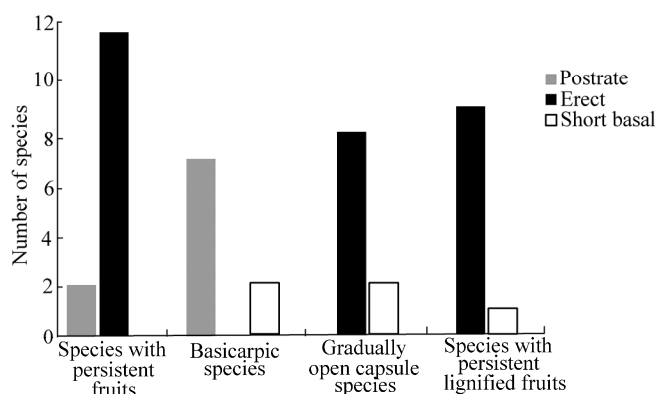


Fig. 4 Number of species in different plant habits and groups of delayed seed dispersal species

Table 3 Relationships between groups of delayed seed dispersal species and antitelochoric mechanisms

Group of seed dispersal species	Myxospermy	Synaptospermy	Trypanocarp	Overall
Basicarpic species	5	2	1	10
Gradually open capsules species	3	1	0	10
Species with persistent fruits	0	13	2	13
Species with persistent lignified fruits	2	1	0	10
Total	10	17	3	43
χ^2	9.558	31.407		
P	<0.050	<0.001		

3.6 Relationships between groups of delayed seed dispersal species and habitats

There was a significant relationship between groups of delayed seed dispersal species and habitats ($\chi^2=18.87$, $df=9$, $P<0.050$). All groups of delayed seed dispersal species were represented in the four types of habitats, except for persistent fruits species that were not present in salt flats. Persistent fruits species were the most common in sand sheets, the Hajar Mountains, and gravel plains. In salt flats, persistent lignified fruits and gradually open capsules species were predominant (Fig. 5).

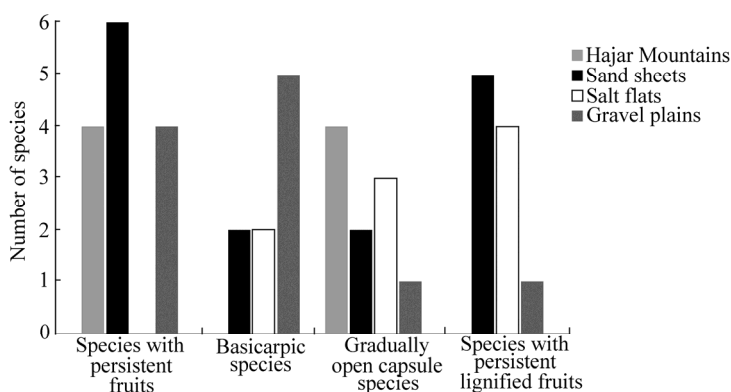


Fig. 5 Number of species in different types of habitats and groups of delayed seed dispersal species groups

4 Discussion

We identified a total of 46 delayed seed dispersal species, which represent around 15.0% of the total studied flora in the desert the UAE (Karim and Fawzi, 2007). All groups of delayed dispersal species described by Martinez-Berdeja et al. (2015) were found in the desert of the UAE except for the species with reproductive dimorphism (amphicarp). Delayed seed dispersal species were

predominantly perennial plants with persistent synaptospermic fruits, which belong to the Fabaceae family, and release fruits in the dry season. It is interesting to note that all graminoids were persistent lignified fruits species, while all prostrate annuals were basicarpic species. The delayed seed dispersal species in the UAE were distributed mainly in sand sheets.

4.1 Delayed seed dispersal species

The significant adaptation of seed retention in desert plants has been discussed in many studies, such as Ellner and Shmida (1981), Lamont et al. (1991), van Rheede et al. (1999), and Lamont and Enright (2000). Delayed seed dispersal is widespread in regions with strongly seasonal climates, poor soil, and recurrent fires (Bastida and Talavera, 2002; Simon and Pennington, 2012). It has also been described in arid and semi-arid regions, where it has been shown to play an important role in protecting seeds against soil-living granivores (Günster, 1994) or desiccation (Pritchard et al., 2004). In the UAE, 46 of the 307 total studied (15.0%) were delayed seed dispersal species. A similar proportion was reported in the Central Namib Desert (13.0%; Günster, 1992). However, Navarro et al. (2009a, b) and Rodríguez et al. (2017) reported 52.9% of the total studied species in the Moroccan High Atlas Mountains, 33.5% in the arid land of southeastern Spain, and 48.0% in the coastal dunes in southern Spain. This result indicates that the number of delayed seed dispersal species is less in hyper-arid hot deserts than in arid and semi-arid Mediterranean (Navarro et al., 2009a, b; Rodríguez et al., 2017).

4.2 Dispersal time of delayed seed dispersal species in seasonal climates

In the unpredictable climate in deserts, rainfall stimulates dehiscence of diaspores by controlling the opening of specific structures such as scales and bracts for some species. Under these conditions, plants regulate the timing of germination to coincide with rainfall time (Günster, 1992; van Rheede et al., 1999). In the UAE, rainfall is temporally unpredictable and usually restricted to a short season (November–March). And we recorded 21 delayed seed species (46.0%) that disperse their seeds in the dry season of the year; i.e., before the arrival of the next rainy season. Similar results have been reported in the Moroccan High Atlas Mountains (Navarro et al., 2009a) and the Mediterranean coastal dunes of Spain (Rodríguez et al., 2017). The high frequency of species that disperse their seeds in the dry season could be explained in the light of the activity of granivores. The species that release their seeds immediately after maturation would be exposed to granivores that are usually active by the end of the fruiting season. It has been reported that the activity of granivores is usually much less in the dry and hot season than in moist cooler season of the year (Molokwu et al., 2010; Gremer and Venable, 2014).

In the Negev and Sinai deserts, all the delayed seed dispersal species (40 species) disperse their seeds in response to rainfall (Guterman, 1994; Guterman and Ginott, 1994). In our study, however, only 9 species released their seeds in response to rainfall. The lower incidence of seed dispersal in the rainy season in the UAE, compared with those in the Negev and Sinai deserts, could be attributed to the regularity and frequency of effective rainfall in the two regions. In the Mediterranean climate of the Negev and Sinai, dispersal in response to rainfall is more advantageous: rainfall is more predictable and thus germination is predicted to happen accordingly (Guterman, 2002). In the arid deserts of the UAE, however, effective rainfall is unpredictable and therefore germination is not predictable (Feulner, 2006). If seeds are dispersed and germinated in response to ineffective rainfall, they might die before reaching the next season (El-Keblawy et al., 1997). In addition, dispersal in the dry season might be advantageous in the UAE as most of the species have innate dormancy (El-Keblawy and Gairola, 2017; El-Keblawy et al., 2018). Seed dispersal in the dry season would help in breaking dormancy as the exposure to the diurnal fluctuation in moisture and temperature is greater on soil surface than on mother plant (El-Keblawy and Bhatt, 2015). Breaking seed dormancy would ensure germination after the arrival of effective rainfall (El-Keblawy, 2014).

4.3 Delayed seed dispersal in sandy and salt habitats

Few studies have assessed the presence of delayed seed dispersal in sand sheets of arid

ecosystems (Wang and Liang, 1995; Liu et al., 2005). In our study, we recorded 25 delayed seed dispersal species in sand sheets (54.0% of the total examined species in that habitat). A high frequency of delayed seed dispersal species reflects the importance of this adaptive mechanism in this habitat. Loose sand being drifted by the wind, which usually happens early in the growing season, is a major problem that buries seeds deep in the soil (Glennie and Evamy, 1968). In addition, early germination exposes seedlings to burial (Peng et al., 2012). Furthermore, the fast water infiltration from the surface soil of sand sheets leaves the top layer dry shortly after rainfall (El-Keblawy and Bhatt, 2015; El-Keblawy et al., 2015). Consequently, delaying seed dispersal in species of sand sheets postpones seed dispersal and germination until the end of windy season, which is in accordance with Liu et al. (2006), Ma and Liu (2008), and Ma et al. (2010). Interestingly, we noticed that many of the delayed seed dispersal species on sand dunes have erect habit (14 out of 25 species). Those species adapt to sand burial on active sand dunes (Günster, 1992).

In our study, delayed seed dispersal species were less occurred in salt flats (23.9%). Similar results were reported in the Central Namib Desert (Günster, 1992). In general, seed germination in salt flats is limited to the period after effective rainfall that dilutes soil salinity. Therefore, the timing of rainfall is the limiting factor that controls successful seedling emergence and establishment in salt flats. Interestingly, all recorded delayed seed dispersal species in salt flats have restricted spatial dispersal, which reflects the special adaptation of the halophytes in salt flats.

4.4 Delayed seed dispersal and spatial dispersal

Delayed seed dispersal species were mainly restricted dispersal species (67.3%), and only 28.7% of the total showed developed spatial dispersal. The high incidence of restricted dispersal within delayed seed dispersal species could be attributed to the heterogeneity of the deserts in the UAE. The distribution of vegetation in the deserts of the UAE is patchy, with few gaps suitable for seedling establishment (El-Keblawy et al., 2015). However, restricted dispersal ensures that seeds are dispersed in safe sites around mother plant (Rodríguez et al., 2017).

Biotic dispersal in arid desert is not a common phenomenon (Shabana et al., 2018). The environmental conditions of such deserts do not support the activities of the biotic vectors (Ellner and Shmida, 1981). Our results indicated that only 8 species (17.4%) adopt biotic dispersal. However, 6 of these 8 species were persistent fruits species (5 species of *Indigofera* genus and *Solanum incanum*), which are distributed by grazing animals. Seeds of these species are dispersed with animal dung and in many cases are able to germinate after their release. Seed passage through animal gut partially breaks down physical dormancy imposed by hard impermeable seed coats and should facilitate subsequent environmental scarification by soil abrasion or extreme temperature cycles (Ortega Baes et al., 2002; Campos et al., 2008).

4.5 Delayed seed dispersal, growth form, and antitelechoric mechanisms

The combination of synaptospermy and delayed seed dispersal would improve seedling establishment and reduce diaspore losses through ant predation (Guterman, 2000, 2001). Species with basicarpy were overspread in all habitats of the hyper-arid deserts of the UAE (Fig. 5). Similarly, Martínez-Berdeja et al. (2015) reported that the basicarpic group was over-represented in the Mojave and Sonoran deserts in California. The basicarpy provide anchorage against surface run-off and protect diaspores from predation (Ellner and Shmida, 1981; van Rheede et al., 1999). Even in years when seed production is low, seed-predation on the basicarpic species is minimal (Ellner and Shmida, 1981). In our results, basicarpic species were mainly annual and prostrate, which is in accordance with Ellner and Shmida (1981), Navarro et al. (2009a), and Martínez-Berdeja et al. (2015).

In our study, 7 graminoids species with persistent lignified fruits were recorded (5 grasses and 2 sedges). It was reported that vegetative shoots of many graminoids, especially perennials, could die in response to weather conditions and with aging (Weaver and Zink, 1946). For example, diaspores of *Setaria verticillata* (Ernst et al., 1992; Cheplick 1998; van Rheede et al., 1999) and

Stipa tenacissima (Haase et al., 1995) remain protected in inflorescence of their mother plant until suitable conditions are available for successful seed germination and seedling emergence.

5 Conclusions

In this study, 15.0% species in the desert of the UAE are delayed seed dispersal species, and most of them preferably distributed in sand sheets. These species were mainly restricted dispersal species, a mechanism that ensures seeds are dispersed in safe sites around mother plant. In the desert of the UAE, delayed seed dispersal species spread seeds until the end of the dry and windy season, thus breaking seed dormancy at this time and ensuring seed germination in the next arrival of the rainy season. This morphological and ecological adaptation of delayed dispersal species is essential to the survival and sustainable development of vegetation in desert environments.

Acknowledgements

The authors would like to thank Prof. Amr Abdel-hamid, Director General of Sharjah Research Academy and special gratitude to Sharjah Seed Bank & Herbarium, Sharjah Research Academy, United Arab Emirates. This work was supported by Sharjah Research Academy, United Arab Emirates.

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Appendix

Table S1 Species with delayed seed dispersal in desert of the UAE

Family or species	Habitat	Group of species	Plant habit	Growth form	Seed storage time (month)	Seed release time	Spatial dispersal	S	T	M
<i>Blepharis ciliaris</i> (L.) B. L. Burtt	GP, M, SS	Species with persistent lignified fruits	SB	PE	7	Rainy	RSD	A	A	P
Aizoaceae										
<i>Aizoon canariense</i> L.	GP, M, SS	Basicarpic species	SB	AN	9	Rainy	RSD	A	A	P
<i>Mesembryanthemum nodiflorum</i> L.	SF	Basicarpic species	PO	AN	9	Rainy & Dry	RSD	A	A	P
Amaranthaceae										
<i>Aerva javanica</i> Juss.	GP, M, SS	Species with persistent fruits	ER	PE	10	Rainy & Dry	DAV	P	A	A
<i>Arthrocnemum macrostachyum</i> (Moric.) K.Koch	SF	Gradually open capsules species	ER	PE	7	Dry	RSD	A	A	A
<i>Halocnemum strobilaceum</i> M.Bieb	SF	Gradually open capsules species	ER	PE	7	Rainy	RSD	A	A	A
<i>Halopeplis perfoliata</i> Bunge ex Schweinf. & Asch	SF	Gradually open capsules species	ER	PE	10	Rainy & Dry	RSD	A	A	A
<i>Suaeda aegyptiaca</i> (Hasselq.) Zohary	SF, SS	Gradually open capsules species	ER	AN	7	Rainy	RSD	A	A	A
Asclepiadaceae <i>Glossonema varans</i> Benth. ex Hook.f.	GP	Gradually open capsules species	ER	PE	6	Rainy & Dry	DAV	P	A	A
Asteraceae										
<i>Anvillea garcinii</i> DC.	SS	Species with persistent lignified fruits	ER	PE	8	Rainy & Dry	RSD	A	A	P
Brassicaceae										
<i>Anastatica hierochuntica</i> L.	SS	Basicarpic species	SB	AN	9	Rainy	RSD	A	A	P
<i>Morettia parviflora</i> Boiss.	GP, M, SS	Species with persistent fruits	ER	PE	7	Dry	RSD	P	A	A
<i>Zilla spinosa</i> Prant	GP, M, SS	Species with persistent fruits	ER	PE	7	Dry	DAV	P	P	A
Caryophyllaceae <i>Sclerocephalus arabicus</i> Boiss.	M, SF, SS	Basicarpic species	PO	AN	9	Rainy & Dry	RSD	A	A	A
Cucurbitaceae										
<i>Citrullus colocynthis</i> (L.) Schrad.	GP, SS	Basicarpic species	PO	PE	7	Dry	RSD	A	A	P
<i>Cucumis prophetarum</i> L.	GP, M	Basicarpic species	PO	PE	7	Dry	RSD	A	A	P
Euphorbiaceae										
<i>Euphorbia larica</i> Boiss.	GP, M	Species with persistent fruits	ER	PE	7	Dry	RSD	P	A	A

To be continued

Continued

Family or species	Habitat	Group of species	Plant habit	Growth form	Seed storage time (month)	Seed release time	Spatial dispersal	S	T	M
<i>Ricinus communis</i> L.	SS	Species with persistent fruits	ER	PE	8	Rainy & Dry	RSD	P	A	A
Fabaceae										
<i>Indigofera arabica</i> Jaub. & Spac	GP, SS	Species with persistent fruits	PO	PE	6	Dry	DBV	P	A	A
<i>Indigofera argentea</i> Burm. f.	GP, SS	Species with persistent fruits	ER	PE	11	Rainy & Dry	DBV	P	A	A
<i>Indigofera caerulea</i> Roxb.	GP, M	Species with persistent fruits	ER	PE	6	Rainy	DBV	P	A	A
<i>Indigofera intricata</i> Boiss.	SS	Species with persistent fruits	PO	PE	11	Rainy & Dry	DBV	P	A	A
<i>Indigofera oblongifolia</i> Forssk	GP, SS	Species with persistent fruits	ER	PE	6	Rainy & Dry	DBV	P	A	A
<i>Medicago laciniata</i> Mill.	GP, M	Basicarpic species	PO	AN	8	Dry	DBV	P	P	A
<i>Trigonella hamosa</i> L.	SS	Basicarpic species	PO	AN	10	Rainy & Dry	DBV	P	A	A
<i>Trigonella stellata</i> Forssk.	GP, M	Basicarpic species	PO	AN	8	Dry	RSD	A	A	A
Juncaceae										
<i>Juncus rigidus</i> Desf.	SF	Species with persistent lignified fruits	ER	GR	9	Dry	RSD	A	A	A
<i>Juncus socotranus</i> (Buchenau) Snogerup	SF	Species with persistent lignified fruits	ER	GR	7	Dry	RSD	A	A	A
Lamiaceae										
<i>Salvia aegyptiaca</i> L.	GP, M	Gradually open capsules species	ER	PE	8	Dry	RSD	A	A	P
<i>Salvia spinosa</i> L.	M	Gradually open capsules species	SB	PE	6	Rainy	RSD	A	A	P
Liliaceae										
<i>Asphodelus tenuifolius</i> Cav.	GP, M, SS	Gradually open capsules species	SB	PE	7	Dry	RSD	A	A	A
Lythraceae										
<i>Lawsonia inermis</i> L.	M, SS	Species with persistent fruits	ER	PE	7	Dry	RSD	P	A	A
Malvaceae										
<i>Abutilon fruticosum</i> Guill. & Perr.	M	Species with schizocarpic fruits	ER	PE	8	Dry	DAV	A	A	A
<i>Abutilon pannosum</i> (G. Forst.) Schldtl.	GP, M	Species with schizocarpic fruits	ER	PE	8	Dry	DAV	A	A	A

To be continued

Continued

Family or species	Habitat	Group of species	Plant habit	Growth form	Seed storage time (month)	Seed release time	Spatial dispersal	S	T	M
<i>Malva parviflora</i> L.	SS	Species with schizocarpic fruits	ER	AN	7	Dry	DAV	A	A	A
<i>Plantago ovata</i> Forssk.	M, SS	Gradually open capsules species	SB	AN	7	Rainy & Dry	RSD	A	A	P
Poaceae										
<i>Aeluropus lagopoides</i> (L.) Trin. ex Thwaites	SF	Retain fruits in dried plants	ER	GR	9	Rainy & Dry	RSD	A	A	A
<i>Cenchrus ciliaris</i> L.	GP, SS	Species with persistent lignified fruits	ER	GR	8	Rainy	DAV	P	A	A
<i>Setaria verticillata</i> (L.) P. Beauv.	GP	Species with persistent lignified fruits	ER	GR	7	Rainy	RSD	A	A	A
<i>Sporobolus ioclados</i> Nees	SF	Species with persistent lignified fruits	ER	GR	8	Dry	RSD	A	A	A
<i>Sporobolus spicatus</i> Kunth	SF, SS	Species with persistent lignified fruits	ER	GR	9	Rainy & Dry	RSD	A	A	A
Polygonaceae										
<i>Rumex dentatus</i> L.	SS	Species with persistent lignified fruits	ER	AN	6	Dry	RSD	A	A	A
Resedaceae										
<i>Ochradenus arabicus</i> Chaudhary, Hillc. & A. G. Mill.	M, SS	Gradually open capsules species	ER	PE	6	Rainy & Dry	RSD	A	A	A
Scrophulariaceae										
<i>Scrophularia deserti</i> Delile	GP, M	Species with persistent fruits	ER	PE	6	Dry	RSD	P	P	A
Solanaceae										
<i>Solanum incanum</i> L.	GP, M	Species with persistent fruits	ER	PE	7	Dry	DBV	P	A	A
Tiliaceae										
<i>Corchorus depressus</i> (L.) Stocks	GP, SS	Basicarpic species	PO	PE	6	Rainy & Dry	RSD	A	A	A

Note: GP, gravel plains; M, Hajar Mountains; SF, salt flats; SS, sand sheets. SB, short basal; PO, prostrate; ER, erect plant; AN, annual; GR, graminoid; PE, perennial; DAV, dispersal by abiotic vectors; DBV, dispersal by biotic vectors; RSD, restricted spatial dispersal; S, synaptospermy; T, trypanocarpy; M, myxospermy; P, present; A, absent.